8

Host and Ecological Relationships of the Parasitic Helminth *Capillaria hepatica* in Florida Mammals

James N. Layne[1]

(Plate I; Text-figures 1-4)

Introduction

The nematode *Capillaria hepatica* (Bancroft, 1893) typically occurs as an adult in the liver of mammals, although in rare instances adult worms may be found in extrahepatic sites. *Capillaria hepatica* is nearly cosmopolitan in its geographic distribution and exhibits broad host tolerance. Although rodents are the principal hosts, the parasite has been found in a number of species in other orders, including Primates, Lagomorpha, Carnivora, and Artiodactyla. Both genuine and spurious human infections have been reported (Ewing & Tilden, 1956; Lubinsky, 1956; MacArthur, 1924; McQuown, 1950, 1954; Otto *et al.*, 1954).

Although *C. hepatica* has been recorded from numerous hosts and localities in North America (Table 1), little is known about its status in populations of particular species or in different habitats or geographic regions. The most comprehensive data presently available on its incidence in natural populations of North American mammals are those of Freeman & Wright (1960) for several species of rodents in Algonquin Park, Ontario, Canada, and Layne & Griffo (1961) for the Florida mouse, *Peromyscus floridanus*. This paper presents additional information on the hosts, geographic and ecologic distribution, and incidence of *C. hepatica* in Florida.

[1]Archbold Biological Station, Lake Placid, Florida 33852 and Department of Mammalogy, The American Museum of Natural History, New York, N.Y. 10024.

Methods and Materials

A total of 2,524 specimens of 27 species of mammals was examined. For the sake of completeness, the sample of *Peromyscus floridanus* reported on previously (Layne & Griffo, 1961) is included in the present analysis.

The majority of the animals was collected by live trapping and killed with ether for examination. Traps were generally set in lines with one or two traps per station and intervals of 30 to 50 ft. between stations, although in some instances traps were set in a 50 or 100 ft. grid. The remaining specimens were obtained by snap or steel trapping, shooting, or as road kills. Data recorded for each specimen usually included locality, date of collection, habitat, sex, age, body weight, external measurements, and reproductive condition.

Occurrence of an infection was based primarily on gross examination of the liver for the characteristic lesions of *C. hepatica* (Pl. I, fig. 1). According to Freeman & Wright (1960), infections of two or more weeks duration should be reliably detected by this method. A further indication of its validity is the fact that use of a formalin-ether concentration technique in the previous study (Layne & Griffo, 1961) did not reveal any infections that had been overlooked during routine autopsy. In the relatively few instances where there was some doubt as to the nature of a lesion, portions of tissue from the area in question were teased apart in a drop of water on a microslide, compressed with a cover slip, and scanned at 100X for the presence of ova (Pl. I, figs. 2 and 3) or fragments of adult worms.

Table I

Summary of North American Host and Locality Records for *Capillaria hepatica*

Host	*Locality and Authority*
Order Primates	
Ateles geoffroyi	Mexico: Chiapas (Caballero & Grocott, 1952); Panama (Foster & Johnson, 1939)
Cebus capucinus	Panama (Foster & Johnson, 1939)
Order Carnivora	
Canis familiaris	U.S.:? Washington, D. C. and vicinity (Wright, 1930)
Order Lagomorpha	
Sylvilagus floridanus	U.S.: Oklahoma (Ward, 1934)
Order Rodentia	
Marmota monax	U.S.: Pennsylvania–zoo specimen (Doran, 1955)
Cynomys ludovicianus	U.S.: Pennsylvania–zoo specimen (Weidman, 1925)
Citellus richardsonii	Canada: Alberta (Brown & Roy, 1943); U.S.: Montana (Luttermoser, 1938)
Sciurus niger	U.S.: Louisiana (McQuown, 1954)
Castor canadensis	U.S.: Washington, D. C.–zoo specimen (Chitwood, 1934)
Thomomys talpoides	Canada: Alberta (Lubinsky, 1956, 1957); U.S.: Wyoming (Dikmans, 1932; Law & Kennedy, 1932–cited from Lubinsky, 1956; Rausch, 1961)
Geomys bursarius	U.S.: Pennsylvania–zoo specimen (Weidman, 1917)
Neotoma cinerea	U.S.: Oregon (Rausch, 1961)
Peromyscus floridanus	U.S.: Florida (Layne & Griffo, 1961; Layne, 1963; present study)
Peromyscus gossypinus	U.S.: Florida (present study)
Peromyscus maniculatus	Canada: Alberta (Lubinsky, 1956, 1957); Ontario (Freeman, 1958; Freeman & Wright, 1960); U.S.: Alaska (Rausch, 1961); New York (Layne, unpublished);? Washington (Dalquest, 1948); artificial infection, species uncertain (Luttermoser, 1938)
Sigmodon hispidus	U.S.: Florida (present study); Texas (Read, 1949)
Clethrionomys gapperi	Canada: Ontario (Freeman & Wright, 1960); U.S.: New York (Fisher, 1963)
Microtus chrotorrhinus	U.S.: New York (Fisher, 1963)
Microtus pennsylvanicus	Canada: Ontario (Freeman & Wright, 1960)
Synaptomys cooperi	Canada: Ontario (Freeman & Wright, 1960)
Lemmus sibiricus	U.S.: Alaska (Rausch, 1961)
Ondatra zibethicus	Canada: Ontario (Freeman & Wright, 1960); Ontario–fur farm (Law & Kennedy, 1932–cited from Lubinsky, 1956; Price, 1931; Swales, 1933); U.S.: Louisiana (Penn, 1942); Maine (Meyer & Reilly, 1950); Michigan (Ameel, 1942)
Mus musculus	U.S.: Maryland (Luttermoser, 1938); Pennsylvania (Doran, 1955)
Rattus rattus	Panama (Calero *et al.,* 1950); U.S.: (Hall, 1916)
Rattus norvegicus	Canada: Quebec (Firlotte, 1948); Panama (Calero *et al.,* 1950) U.S.: Illinois (Wantland *et al.,* 1956); Maryland (Calhoun, 1962; Davis, 1951; Habermann *et al.,* 1954; Luttermoser, 1936; Shorb, 1931; Yokogawa, 1920); New York (Herman, 1939); North Carolina (Harkema, 1936); Pennsylvania (Herman, 1939); Washington, D. C. (Cram, 1928; Price & Chitwood, 1931).
Rattus rattus or *R. norvegicus*	U.S.: California;? Pennsylvania; Rhode Island; Washington, D.C. (Hall, 1916)
Napaeozapus insignis	Canada: Ontario (Freeman & Wright, 1960)
Order Artiodactyla	
Tayassu pecari	Panama (Foster & Johnson, 1939)
Sus scrofa	U.S.: domestic–artificial infection (Tromba, 1959)

Infections were rated as to severity on the basis of the appearance and abundance of lesions. Luttermoser (1938) considered the extent of lesions rather than actual egg counts to be better as an index of degree of infection. Cases in which the liver had small, discrete, and widely scattered lesions, often confined to a single lobe, were regarded as light. Infections in which the lesions were more numerous and extensively distributed were classified as moderate, whereas those in which the lesions were almost continuous and involved most or all of the hepatic lobes were rated as heavy.

Collections were made in 22 counties of the state, with emphasis on the north-central region. An attempt was made to sample as wide a range of habitats as possible. Although specimens were taken only casually (*e.g.* as road kills) in some habitat types, over 20 distinct vegetative types were systematically live trapped or snap trapped for small rodents. For present purposes these may be grouped under nine major categories which are briefly described below. More detailed descriptions of most of these may be found in Carr (1940), Laessle (1942, 1958), and Rogers (1933). Rogers (1933) and Cooper *et al.* (1959) also give data on air and soil temperatures and evaporation rates for some of the habitats included here.

1. *Hammocks.* Mixed hardwood forests, including mesophytic, upland, live oak, and cabbage palm hammocks. The first of these has laurel oak *(Quercus laurifolia)*, magnolia *(Magnolia grandiflora)*, and American holly *(Ilex opaca)* as characteristic tree species. The soils are rich in organic matter and usually moist. Upland hammocks are drier than the preceding, with laurel oak, southern red oak *(Q. falcata)*, persimmon *(Diospyros virginiana)*, mockernut hickory *(Carya tomentosa)*, and loblolly pine *(Pinus taeda)* being representative tree species. Live oak hammocks, with live oak *(Q. virginiana)* as the dominant tree and generally sparse ground cover, are also comparatively xeric. Cabbage palm hammocks sampled consisted of dense stands of cabbage palm *(Sabal palmetto)* and other trees and shrubs. Soils were rich and moist.

2. *Pine-oak woodlands.* Generally open stands of pines and oaks occurring on sandy well-drained soils, often on low ridges or hills. Ground cover is generally rather sparse resulting in frequent patches of exposed sand. Two types of pine-oak woodlands were sampled in the study, one with longleaf pine *(Pinus palustris)* and turkey oak *(Q. laevis)* as the chief tree species, and the other with slash pine *(P. elliottii)* and turkey oak. The first is widespread throughout much of Florida, while the second is restricted to a relatively small area in the south-central part of the peninsula. Slash pine-turkey oak woodlands are somewhat intermediate between longleaf pine-turkey oak woodlands and sand pine scrub, described below, in over-all species composition and environmental conditions. Only one of 18 different pine-oak woodland habitats from which collections were made represented slash pine-turkey oak.

3. *Scrub.* Stands of scattered pines with a dense understory of small trees and shrubs, a number of which are sclerophyllous. Herbaceous ground cover is typically sparse, and open sandy patches are common. This comparatively xeric vegetative type occurs on excessively well-drained fine sandy soils. Sand pine *(P. clausa)* is generally regarded as the most characteristic species of true scrub, and myrtle oak *(Q. myrtifolia)*, live oak, and Chapman oak *(Q. chapmanii)* are the principal elements of the shrub layer. For purposes of the present study, one station (Levy-19) with all of the characteristics of scrub except for slash instead of sand pine is included under this category.

4. *Flatwoods.* Level pinelands found on poorly drained soils. The particular species of pine present as the dominant tree depends upon edaphic conditions. Longleaf pine is typical of better drained sites and slash pine of the more moist areas. Ground cover in flatwoods is usually dense, consisting of varying proportions of grasses, palmettos, and forbs. Shrubs and deciduous trees range from rare to abundant enough to form a distinct understory, depending on frequency of fire.

5. *Swamps.* Cypress *(Taxodium distichum)* and hardwood swamps and bayheads. The latter are low, moist to wet, dense stands of various trees, shrubs, and vines. Sweetbay *(Magnolia virginiana)* and loblolly bay *(Gordonia lasianthus)* are common species of bayheads.

6. *Wetlands.* Moist to wet prairies, marshes, and lush herbaceous and brushy borders of roadside ditches and ponds.

7. *Dunes.* Coastal sand dunes generally sparsely vegetated with sea oats *(Uniola paniculata)* and various other grasses and forbs.

8. *Ruderal.* Old fields in early successional stages, pine plantations, weedy or grassy road shoulders, and fence rows.

9. *Miscellaneous.* Buildings and lawns or gardens in agricultural or residential areas. Except for snap trapping for *Mus musculus* and *Rattus*, no systematic collecting was carried out in these habitats.

Although in many cases a given locality was sampled only once, periodic trapping of selected

Table II

Species and Numbers of Florida Mammals Examined for *Capillaria hepatica*

Asterisk Indicates Habitat or Locality from which Infections were Recorded

Species	No. exam.	Habitat[1]	Locality[2]
Didelphis marsupialis	6	H1, P1, S1, U3	A3, H1, Lv1, U1
Scalopus aquaticus	5	P1, M2, U2	A4, La1
Cryptotis parva	10	P1, F6, W1, R2	A10
Blarina brevicauda	6	H3, W3	A5, H1
Sylvilagus floridanus	12	H7, S1, F1, R2, U1	A3, B1, H7, Le1
S. palustris	4	W3, R1	A1, Lv1, Pi2
Sciurus carolinensis	11	H4, M2, U5	A8, H1, Lv1, Pi1
S. niger	2	P1, F1	A1, Lv1
Glaucomys volans	2	R1, M1	A2
Geomys pinetis	9	P3, S1, R4, U1	A1, G1, H2, Lv4, St1
Oryzomys palustris	32	S7, F5, W17, R2, M1	A7, H6, Le5, Lv13
Peromyscus polionotus	43	P3, S2, F1, D34, R3	A3, B3, E30, H6, O1
P. gossypinus	254	H39, P19, S126*, F9, Sw32*, W1, R1, U5	A55, B12, Fr7, H38, Lv141*, St1
P. floridanus	1312	H246*, P400*, S600*, F61, R16, U1	A634, C4, G18, H75*, Lv570*, Pa6, Pu1, St4*
Reithrodontomys humulis	2	P2	A2
Ochrotomys nuttalli	12	H3, P5, S4	A4, H2, Le2, St4
Sigmodon hispidus	427	H3, P32, S200*, F66, Sw18, W40, D9, R51*, U8	A123, B4, E6, H36*, Le11, Lv213, Pi27, St6, W1
Neotoma floridana	2	H1, S1	Lv1, T1
Neofiber alleni	9	W9	A3, H5, Pu1
Rattus norvegicus	1	M1	Dw1
Rattus rattus	18	R4, M11, U3	A2, Du2, M2, Pi12
Mus musculus	328	H7, P1, S3, W13, D3, R2, M297, U2	A303, H3, Le19, O3
Urocyon cinereoargenteus	6	H1, P1, U4	A3, F1, H1, Pu1
Procyon lotor	5	S1, R1, U3	A1, H1, Lv1, M2
Mustela frenata	1	U1	Du1
Mephitis mephitis	1	D1	De1
Lynx rufus	4	H1, R1, U2	A2, De1, T1

[1]Habitat Key: H—hammocks, P—pine-oak woodlands, S-scrub, F—flatwoods, Sw—swamps, W—wetlands, D—dunes, R—ruderal, M—miscellaneous, U—unknown. Number of specimens examined from given habitat type follows abbreviation.

[2]Locality (county) Key: A—Alachua, B—Brevard, C—Clay, De—DeSoto, Du—Duval, E—Escambia, F—Flagler, Fr—Franklin, G—Gilchrist, H—Highlands, La—Lake, Le—Lee, Lv—Levy, M—Monroe, O—Okaloosa, Pa—Palm Beach, Pi—Pinellas, Pu—Putnam, Sa—Santa Rosa, St—St. Johns, T—Taylor, W—Walton, U—Unknown. Number of specimens examined from given county follows abbreviation.

pine-oak woodland, scrub, flatwoods, hammock, and ruderal habitat types was conducted in order to obtain data on seasonal and long-term trends in prevalence of *C. hepatica* in small mammal populations. The numbers of samples obtained from a given station ranged from two in a two-year period to 21 over an eight-year interval.

Results

Host and geographic distribution. The species and numbers of mammals examined for *C. hepatica* and localities represented are listed in Table 2. Eight per cent of the 2,524 specimens and 11% (3) of the 27 species examined had *Capillaria* infections. The species and localities from which infections were recorded included the Florida mouse, *Peromyscus floridanus*, from Highlands, Levy, and St. Johns Counties; the cotton mouse, *Peromyscus gossypinus*, from Levy County; and the cotton rat, *Sigmodon hispidus*, from Highlands and Levy Counties. *C. hepatica* has not been previously reported from the cotton mouse, and *Sigmodon* constitutes a new host record for Florida and the southeastern United States generally.

Based on total numbers of specimens examined from all habitats combined, incidence of infection was 15.4% in *P. floridanus*, 6.3% in *P. gossypinus*, and 10.5% in *Sigmodon*. Because infection rates in populations in the same and different habitats varied considerably and sample sizes are unequal, these values probably do not reflect the true status of *C. hepatica* in these species as well as a mean incidence calculated from individual population means. Expressed in the latter manner, incidence was 13.2% in Florida mice, 2.5% in cotton mice, and 6.3% in cotton rats.

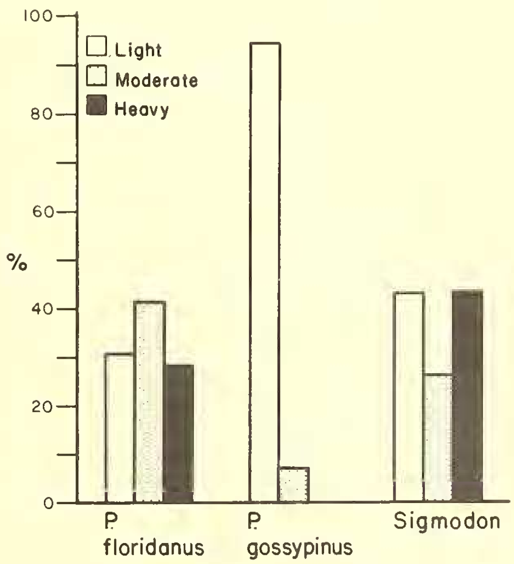
Considering only those localities from which infected animals of any species were collected (Table 3), prevalence of *C. hepatica* was 34.2% in Florida mice, 14.8% in cotton mice, and and 21.1% in cotton rats. As there are significant differences in the probability of infection in different age groups, the above values may be influenced by different age compositions of the samples of each species. Thus incidence based only on adult animals is probably a more satisfactory value for comparative purposes. Adult infection rates in *P. floridanus*, *P. gossypinus*, and *Sigmodon* were 37.7%, 14.8% and 30.8%, respectively. Neither the total nor adult infection rates in *P. floridanus* and *Sigmodon* differ statistically when tested by chi-square ($P > .05$), but both species differ significantly from *P. gossypinus* ($P < .005$).

Florida mice and cotton rats tended to be more heavily infected than cotton mice (Text-fig. 1). The difference in severity of infections between *P. gossypinus* and the other species is significant ($P < .05$), but *P. floridanus* and *Sigmodon* do not differ significantly in the proportions of light, moderate, and heavy infections.

With one exception, all infections of *C. hepatica* observed in this study were localized in the liver as is typical. However, one cotton rat with a massive early infection of the upper hepatic lobes also had scattered adult worms in the mesentery of the spleen and a "knot" of worms about ¼-inch in diameter in the mesentery adjacent to the liver. The worms at the latter site appeared to be dead and in the process of becoming calcified. No ova were observed when teased fragments of the worms were examined microscopically.

Infected livers of *P. floridanus* differed markedly in appearance from those of the other species. Even in the case of the lightest infections, the livers of Florida mice became prominently lobulated, contrasting greatly with the normally smooth surface of the organ (Pl. I, fig. 1). Although the liver of one heavily infected cotton rat had a slightly lobulated appearance, all other infected livers of *Sigmodon* and cotton mice were normal in appearance except for the presence of lesions.

Ecological distribution. Infected mice were recorded from five (hammocks, pine-oak woodlands, scrub, swamps, and ruderal) of the nine



TEXT-FIG. 1. Severity of infections of *C. hepatica* in three Florida rodent species.

TABLE III

INCIDENCE OF *Capillaria hepatica* INFECTIONS IN POPULATIONS OF THREE RODENT SPECIES

Habitat and Locality	*P. floridanus* Total N ex.	N inf.	%	Adults N ex.	N inf.	%	*P. gossypinus* Total N ex.	N inf.	%	Adults N ex.	N inf.	%	*Sigmodon* Total N ex.	N inf.	%	Adults N ex.	N inf.	%
Scrub																		
Highlands—12	19	7	36.8	18	7	38.9	6	0	0	6	0	0	16	0	0	16	0	0
Levy—1	7	2	28.6	3	2	66.7	1	0	0	1	0	0	30	4	13.3	14	4	28.6
Levy—3	11	7	63.6	8	5	62.5	—	—	—	—	—	—	2	0	0	2	0	0
Levy—10	203	23	11.3	177	22	12.4	10	4	40.0	8	3	37.5	40	4	10.0	29	4	13.8
Levy—19*	213	126	59.2	178	116	65.2	70	12	17.1	55	12	21.8	86	32	37.2	50	27	54.0
Levy—28	82	30	36.6	76	29	38.2	22	0	0	22	0	0	17	3	17.6	6	3	50.0
St. Johns—23	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
St. Johns—24	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Slash pine-turkey oak Highlands—13	53	4	7.5	33	3	9.3	7	0	0	7	0	0	1	1	100.0	1	1	100.0
Ruderal (grassy) Highlands	—	—	—	—	—	—	—	—	—	—	—	—	19	1	5.3	10	1	10.0
Hammock (live-oak) St. Johns—24	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Swamp (bayhead) Levy—19	—	—	—	—	—	—	9	1	11.1	9	1	11.1	2	0	0	2	0	0

*Typical scrub vegetation but with slash instead of sand pine as noted in text.

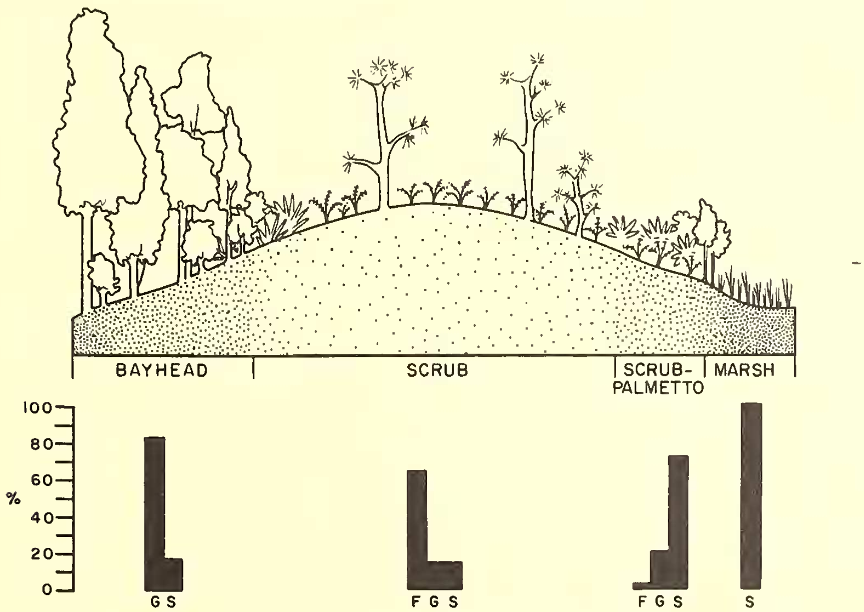
major habitat categories sampled (Table 2). Including all mammals obtained from all habitats combined, over-all infection rates were 0.3% in hammocks, 1.1% in pine-oak woodlands, 26.0% in scrub, 2.0% in swamps, and 1.1% in ruderal situations. The data thus reveal a strong preponderance of infections in scrub habitats. This indication of habitat specificity in the occurrence of *C. hepatica* is further strengthened when the data are examined in greater detail. All non-scrub habitats from which infected animals were collected were located within dispersal distance of scrubs with moderate to high incidence of *C. hepatica.*

Data from a locality in Levy County (Levy —19) that was studied over an eight-year period provide a particularly clear example of the close correlation between the occurrence of *C. hepatica* and scrub environments. The scrub vegetation at this site was restricted to a slightly elevated area and graded abruptly into surrounding low bayhead and marsh habitats (Text-fig. 2). Of the 418 mammals examined from this area, 46% of those collected in the scrub were infected as compared to only 2% from the adjacent habitat types. It is also likely that the infected animals from the adjoining habitats had acquired their infections in the scrub.

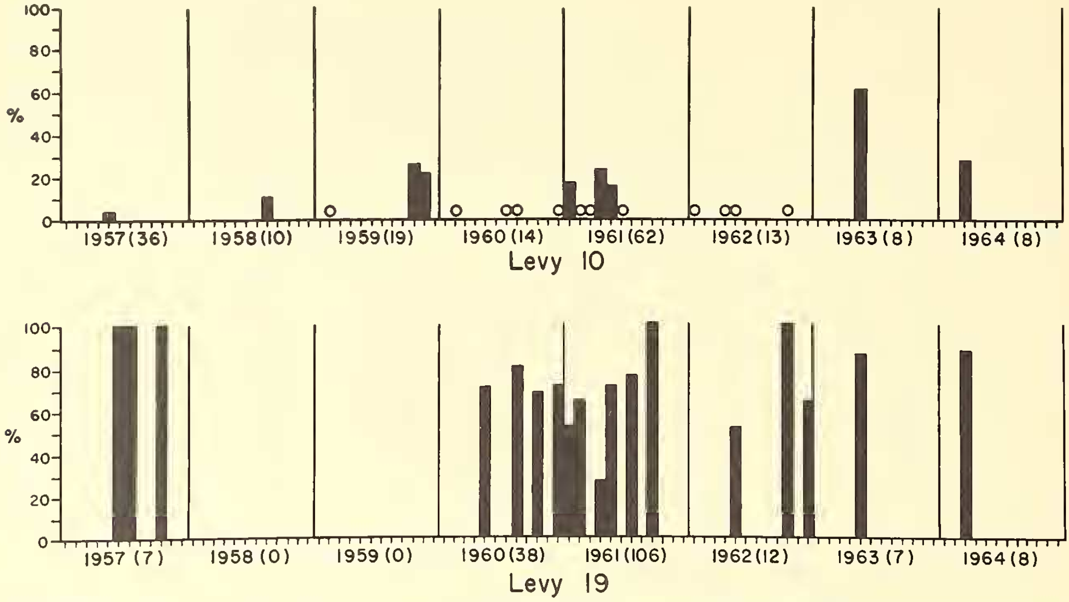
Table 3 summarizes data on prevalence of *Capillaria* in the three rodent species at all stations in which infections occurred in at least one of the species. The incidence of infections is strongly correlated with the extent to which a species occurs in scrub and its general abundance in this habitat. The data also indicate considerable intraspecific variation in infection rates within a given habitat type. Such variability tends to be greater in *Sigmodon* and *P. gossypinus* that in *P. floridanus,* with the last species also exhibiting consistently higher infection rates. There also appears to be some tendency in at least the Florida mouse and cotton rat for infection rates at different stations to vary in the same direction.

Geographic differences in infection rates in different species or populations of the same species are not apparent from the present data. There was as much variation in inter- and intraspecific infection rates between stations 1, 3, 10, 19, and 28 in Levy County, all of which are within 5 miles of one another, as between those in different parts of the state.

Multiple samples from the same station show yearly fluctuations in incidence of *Capillaria.* However, there is some evidence from two *P. floridanus* scrub populations sampled over an eight-year period that infection levels in a given population may vary within relatively narrow limits for a considerable span of time (Text-fig. 3). The two populations in question are located only about 5 miles apart, yet are separated by unsuitable habitat.



TEXT-FIG. 2. Relationships of habitats at station Levy-19 and host species composition in each. Corresponding data on infection rates given in text. Density of stippling indicates degree of soil moisture; vertical scale somewhat exaggerated. Symbols: F = *P. floridanus,* G = *P. gossypinus,* S = *Sigmodon hispidus.*



TEXT-FIG. 3. Prevalence of *C. hepatica* infections in adult *P. floridanus* in two nearby scrub habitats from 1957 to 1964. Samples examined each year are given in parentheses following year.

Sex and age differences in infections. Table 4 gives the sex and age distribution of *C. hepatica* in infected host populations. The age classes used for the two *Peromyscus* species are based on pelage features. Mice assigned to the juvenile age class were still in the full gray juvenile pelage and showed no sign of molt on the dorsum. Individuals undergoing the dorsal phase of the postjuvenile molt were regarded as subadults, while mice in which the postjuvenile molt had been completed were assigned to the adult class. Approximate chronological ages corresponding to these pelage phases are under 6 weeks for juveniles, 6 to 13 weeks for subadults, and over 14 weeks for adults (Layne, 1966; Pournelle, 1952). Age classes of cotton rats were based on body weight as follows: juvenile, less than 40 g; subadult, 40-70 g; and adult, above 70 g.

A relationship between age and infection rate is evidenced by all species. No parasitized juveniles were found in any species, although samples of this age class are admittedly small. Adult infection rates are significantly higher ($P < .05$) than those of subadults in both Florida

TABLE IV
SEX AND AGE DIFFERENCES IN *Capillaria hepatica* INFECTIONS

Species	Age class	*Male* N ex.	N inf.	%	*Female* N ex.	N inf.	%	*Total* N ex.	N inf.	%
P. floridanus	Juvenile	10	0	0	16	0	0	26	0	0
	Subadult	40	9	22.5	28	4	14.3	67	13	19.4
	Adult	236	98	41.5	262	91	34.7	498	189	38.0
P. gossypinus	Juvenile	4	0	0	2	0	0	6	0	0
	Subadult	3	0	0	8	0	0	11	0	0
	Adult	37	12	32.4	26	4	15.4	63	15	23.8
Sigmodon	Juvenile	17	0	0	11	0	0	28	0	0
	Subadult	19	3	15.8	33	2	6.1	52	5	9.6
	Adult	57	16	28.0	52	23	44.2	109	39	35.8

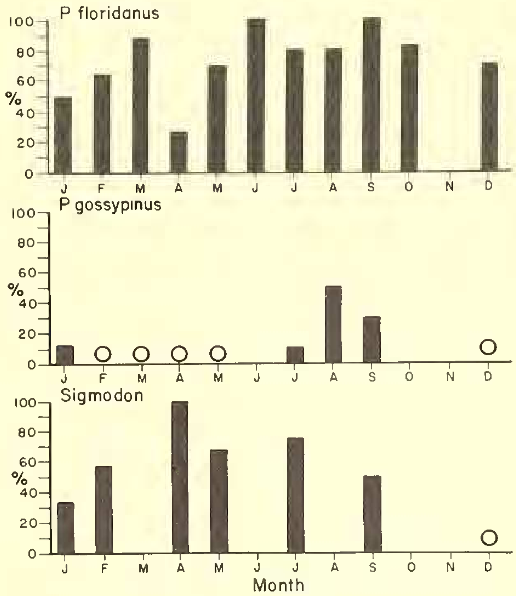
mice and cotton rats. An age effect in infection rate also appears to persist into the adult class of *P. floridanus*. Thirty-one nonparasitized males from infected populations had a mean weight of 28.2 g, while mean weight of 28 parasitized males was 35.0 g. Corresponding values for 37 noninfected females and 12 infected females were 29.5 g and 34.7 g respectively. It thus appears that infections are more prevalent in older adults, assuming at least a rough correlation between weight and age in these field populations.

With the exception of adult cotton rats, more males than females in each species and age group had *C. hepatica*. Although the differences are not statistically significant ($P > .05$) in any case, they are suggestive and may reflect larger activity ranges in males than females.

Seasonal variation in infections. Monthly infection rates in adult *P. floridanus, P. gossypinus,* and *Sigmodon* from one extensively sampled scrub locality (Levy—19) are shown in Text-fig. 4. The graphs are based on composite samples representing eight years of collecting and thus reveal only average trends.

In the Florida mouse, infections appear to be relatively low during the winter months and to increase during summer and early fall. Although the data are limited, a similar seasonal trend is suggested for *P. gossypinus*. Peak levels of infection in *Sigmodon*, however, appear to come in the spring, although incidence during the winter months tends to be low as in the case of the two *Peromyscus* species.

Relationship between incidence and host density. Population levels and infection rates in two scrub populations of *P. floridanus* are compared in Table 5. The number of mice captured per 100 trap-nights is employed as the index of



TEXT-FIG. 4. Seasonal variation in adult infection rates at a single scrub station (Levy-19).

TABLE V

RELATIONSHIP BETWEEN POPULATION LEVEL AND INCIDENCE OF *C. hepatica* IN ADULTS OF TWO *P. floridanus* POPULATIONS

Station 10				Station 19			
Month and year	Pop. index (mice/100 trap-nights)	N	Adult Inf. rate (%)	Month and year	Pop. index (mice/100 trap-nights)	N	Adult Inf. rate (%)
Jan. 1961	49*	12	16.6	May 1960	20*	10	70.0
Jan. 1962	53*	2	0	May 1961	28*	17	70.5
Feb. 1959	48**	10	0	May 1963	6*	7	85.7
Feb. 1961	91*	6	0	July 1957	5*	4	100.0
May 1957	26**	36	2.8	Aug. 1960	17*	9	80.0
May 1961	24*	7	14.3	July 1961	14*	7	75.0
Apr. 1962	51*	9	0	Oct. 1960	21*	11	66.6
May 1963	16*	8	62.5	Sept. 1961	2*	1	100.0
Aug. 1958	38**	10	10.0	Dec. 1960	17*	9	70.0
Aug. 1960	23*	5	0	Dec. 1962	10*	5	62.5

*Trapline with 2 traps/station
**100 ft. grid, 1 trap/station

mouse abundance. The combined data for the two localities suggest a negative correlation between host abundance and degree of parasitism in this species. Station 10, with an over-all population index of 42 mice per 100 trap-nights, had a mean infection rate of 10%, as compared to station 19 with a mean population index of 14 and an adult infection rate of 78%. A similar relationship is evident within each population when comparison is made between abundance and infection rates at the same season in different years.

Discussion

This study indicates that *Capillaria hepatica* is a relatively localized and uncommon parasite of Florida mammals, yet probably is rather widely distributed in the state. While records were obtained from only three of the 22 counties in which collecting was done, these localities are widely separated, Levy and St. Johns Counties being located on opposite sides of the northern part of the peninsula and Highlands County in the south-central part of the state.

Levels of infection previously reported in rodents in North America vary greatly (Table 6), although variations in sampling techniques and methods of reporting results make critical comparisons and interpretations difficult. In general, the present data suggest that the parasite occurs with greater frequency in *Rattus,* particularly urban populations, than in native species. Compared to other native rodents, the incidence of *C. hepatica* in the three Florida species is relatively high. This is particularly true of *P. floridanus* and *Sigmodon*. The greater infection rate given for the Florida mouse in this paper compared to that reported earlier (Layne & Griffo, 1961) is due to additional collecting of this species being concentrated in areas with higher rates of infection. This in itself illustrates the

Table VI

Reported Infection Rates of *C. hepatica* in North America Rodents

Species	*Locality*	*Incidence, per cent*	*Source*
Sciurus niger	Louisiana	3.7	McQuown, 1954
Peromyscus maniculatus	Ontario	9.4	Freeman & Wright, 1960
*P. maniculatus**	Washington	"virtually all"	Dalquest, 1948
P. floridanus	Florida	2.9	Layne & Griffo, 1961
P. floridanus	Florida	15.4	Present study
P. gossypinus	Florida	6.3	Present study
Sigmodon hispidus	Florida	10.5	Present study
Clethrionomys gapperi	Ontario	2.8	Freeman & Wright, 1960
Ondatra zibethicus	Louisiana	less than 10-ca. 50	Penn, 1942
O. zibethicus	Maine	17+	Meyer & Reilly, 1950
O. zibethicus	Michigan	3	Ameel, 1942
Mus musculus	Maryland	4	Luttermoser, 1938
Rattus norvegicus	Quebec	6	Firlotte, 1948
R. norvegicus	Maryland	85.6	Luttermoser, 1936
R. norvegicus	Maryland	47.9	Shorb, 1931
R. norvegicus (semi-wild)	Maryland	53.3	Calhoun, 1962
R. norvegicus (semi-wild)	Maryland	35	Habermann *et al,* 1954
R. norvegicus	Maryland	94.1	Davis, 1951
R. norvegicus	New York	73.5	Herman, 1939
R. norvegicus	Pennsylvania	<30	Herman, 1939
R. norvegicus	North Carolina	2.6	Harkema, 1936
R. norvegicus	Washington, D. C.	77	Price, 1931
R. norvegicus (396) + *R. rattus* (4)	Panama	12	Calero *et al,* 1950

*Parasite not identified in paper but from description almost assuredly *C. hepatica*.

problems involved in attempting to assess the real significance of differences in incidence values given by various authors.

Herman (1939) noted that few of the infected *Rattus norvegicus* examined from the New York Zoological Park had the entire liver affected by lesions and that in only 14% was more than half of the organ involved. Luttermoser (1936) similarly observed that infections in Baltimore rats were of low intensity. Assuming generally comparable criteria of extent of infection in the above and present studies, both Florida mice and cotton rats appear to have a greater proportion of heavy infections than *Rattus*. Dalquest (1948), presumably referring to *C. hepatica*, stated that virtually all *P. maniculatus* collected on Jones Island in the San Juan Island group off the coast of Washington had greatly swollen livers with a yellow, crystalline appearance. This description would appear to fit the category of heavy infection as used in this study. These limited data suggest that native rodents may tend to acquire more intense infections of *C. hepatica* than *Rattus*.

An earlier study (Layne & Griffo, 1961) revealed *C. hepatica* to be almost entirely confined to populations of the Florida mouse living in scrub or similar habitat types. The present data, representing numerous other potential host species and more extensive locality and habitat sampling, provide further confirmation of a highly restricted ecological distribution for this parasite in Florida. All of the infected specimens of the three host species were collected in scrub or similar habitats or from other habitats located near scrub from which infected animals could readily disperse. The over-all incidence of infection in each species also is clearly correlated with the extent to which it is found in scrub habitats. Of the three species, the Florida mouse is most characteristic of scrub and has the highest incidence of *C. hepatica*. Cotton mice and cotton rats occur more commonly in other habitats. In the present study, cotton rats were more abundant in scrub than cotton mice. In addition, live trapping data from permanent study plots indicated that cotton rats living in scrub tend to be more sedentary than cotton mice, many of the latter trapped in this habitat appearing to be transient individuals. This may explain the relatively low incidence and intensity of *C. hepatica* infections in *P. gossypinus* even from scrub stations with unusually high incidence of the parasite in *P. floridanus* and *Sigmodon* populations.

The pronounced habitat specificity of *C. hepatica* in Florida is not evident in other parts of the species' range. Rather, the great ecological diversity represented by its known hosts in North America (Table 1) and elsewhere together with its extensive geographic range suggest broad environmental tolerance. Furthermore, specific information on habitat relationships in other parts of the range indicates that, unlike the case in Florida, the parasite tends to have higher prevalence in more moist habitat types (Freeman & Wright, 1960; Pavlov, Skrjabin *et al.*, 1957, cited from Freeman & Wright, 1960).

The basis of the marked restriction in the ecological distribution of *C. hepatica* in Florida is far from clear. Among the factors that might be involved are distribution of suitable hosts, substrate characteristics, host population dynamics, methods of egg-relcase and dissemination, and feeding habits of potential hosts.

There does not appear to be any strong correlation between the ecologic distribution of *C. hepatica* and mammalian hosts in Florida. The wide variety of known hosts of this parasite indicate that any of the small rodents involved in this study would serve as a suitable host. Moreover, the species often found infected in scrub or similar habitats also commonly occurred singly or in combination in other habitat types from which *C. hepatica* was only rarely or never recorded. In a number of cases such habitats were actually continuous with scrub with a high incidence of the parasite.

It is possible that scrub soils provide better conditions for survival or embryonation of eggs released from livers of the host than those of other habitats included in this survey. In view of the wide geographic range of the parasite and the variety of its recorded hosts, it does not seem likely that substrate conditions would have such an important influence on its ecologic distribution in Florida. Furthermore, if substrate conditions are so critical, it is difficult to reconcile the evidence for preferences for moist conditions in other parts of the range with high incidence in very sandy, highly drained soils in Florida. The picture is further complicated by the fact that *C. hepatica* appears to be completely absent from longleaf pine-turkey oak woodlands which are also characterized by sandy, well-drained soils, although there are important structural and chemical differences between the soils of these habitats and true scrub.

Freeman & Wright (1960) believed that population density played an important role in determining the incidence of *C. hepatica* in small rodents in a local area in Ontario. Although host population level may be an important factor influencing establishment or persistence of *C. hepatica* in certain habitats included in this study, there is no convincing evidence that it is a major cause of the observed habitat distribution of the parasite. Scrub and related habitat types in which infections occurred did not consistently support higher populations of small rodents than other habitats from which infections were never reported; nor does there seem to be any significant correlation between host abundance and infection rate at different stations in scrub habitat. In fact the data suggest an inverse relationship. On the other hand, small rodents are often scarce in longleaf pine-turkey oak woodlands, and although other aspects of the habitat might be suitable for *C. hepatica*, the low host density might make establishment and maintenance of the parasite difficult. Opposed to this argument, however, is the fact that some of the scrub habitats and the single slash pine-turkey oak woodland station studied over a period of several years at times had populations as low or lower than some longleaf pine-turkey oak stations yet maintained relatively high levels of *C. hepatica* infections. Possibly the interval of host scarcity is the critical factor in this situation; evidence indicates that periods of continuous low population density may be considerably more prolonged in longleaf pine-turkey oak habitats.

Laboratory studies on the life cycle of *C. hepatica*, reviewed by Freeman & Wright (1960) and Wright (1961), indicate that infections are acquired through ingestion of infective ova released from the liver of another host through cannibalism, predation, or natural death and decomposition. Ova freed through decomposition of the liver require a longer period for embryonation and have lower viability than those passed through the alimentary tract of another animal.

Although little is known of the actual details of the life cycle under natural conditions, it is logical to assume that cannibalism and predation are the most important of the commonly accepted egg-disseminating mechanisms. Freeman & Wright (1960) concluded that cannibalism in communal winter nests, rather than predation, was the chief source of infections in deer mice in Ontario, although their evidence was entirely circumstantial and subject to other interpretations.

Cannibalism does not appear to be an important egg-releasing mechanism in Florida mammals. Field data provide no evidence of communal nesting or cannibalism in any of the three host species, nor is there any reason to suppose that if these phenomena were common they would be more prevalent in scrub than other habitat types in which the species are found. This leaves predation as the more likely method of egg-dissemination.

All other things being equal, higher predation levels would seem to contribute to maintaining *C. hepatica* in a small mammal population by insuring a continuous supply of infective ova. Present data are far too limited to allow definitive conclusions concerning relative predator abundance in the various habitats sampled. However, casual observations gave the impression that potential small mammal predators such as bobcats, foxes, raccoons, opossums, skunks, feral pigs, snakes, and birds of prey tended to be more common in scrub than in many of the habitats studied. In fairness, it should be noted that predator sign was probably more easily observed in scrub than in some of the other habitats studied. As in the case of rodent population levels, however, abundance of potential predators was by no means associated only with scrub habitats and thus cannot fully explain the high incidence of *C. hepatica* there. Furthermore, as some of the scrubs with high incidence of *C. hepatica* were small, many of the vertebrate predators occurring there probably ranged over other habitat types in the vicinity, thus providing opportunity for wider dispersal of ova from infected rodents eaten.

Certain aspects of the feeding behavior of Florida mice, cotton mice, and cotton rats in scrub seemed to be more specific to this habitat type than the factors mentioned above. The two *Peromyscus* species are essentially granivorous in their dietary whereas the cotton rat is typically herbivorous. However, field observations indicate that all three species have generally similar feeding habits when living in scrub. Acorns appear to be an important food source in scrub. They are generally abundant in late fall and early winter and decline steadily through winter and spring. The rodent populations follow the same annual cycle of abundance and decline. As mast supplies become scarce in late winter and spring, there is much evidence of digging by the rodents for food. This behavior would seem to increase the probability of exposure to infective ova in the soil.

A preliminary attempt to obtain actual evidence for this hypothesis in a scrub habitat (Levy –19) with an unusually high level of *C. hepatica* was unsuccessful. Fifty soil samples from the surface to a depth of about 2 inches were collected, many from within and around pits dug by foraging mice, and examined microscopically for ova. In addition, feces and stomach contents of 30 *P. floridanus*, the species with the highest incidence of infections at this station, were also surveyed for eggs in the hope that the presence of ingested eggs together with food remains would provide some clue to the source of infections. No ova were detected in either case.

None of the above factors seems adequate alone to account for the narrow habitat specificity of *C. hepatica*. It is possible, therefore, that the ecologic distribution of *C. hepatica* is due to a particular combination of such factors which has a much higher probability of occurrence in scrub than other habitat types. This set of conditions might include 1) substrate suitable for survival of ova, 2) sufficiently stable and high enough populations of potential host species to insure continuance of the cycle of parasitism, 3) an abundant enough supply of small mammal predators to insure an adequate supply of infective ova, and 4) host foraging behavior conducive to exposure to ova. Although this explanation is more consistent with the present data than a single factor model, it is still difficult to conceive of an interaction of a number of factors being responsible for the sharply delimited habitat distribution of *C. hepatica*. Thus, although such a combination of conditions as noted above may be generally prerequisite for the occurrence of the parasite, some additional feature unique to scrub and related habitats may actually be the critical factor permitting its establishment and maintenance.

Such a factor may be the presence of some invertebrate species, most likely an insect, in scrub habitats which may play a key role in the transmission of the parasite. It may supplement or replace vertebrate predators as the chief egg releasing and disseminating agent through feeding on dead mice or on feces of predators which have eaten infected mammals. It may increase probabilities of accidental ingestion of *C. hepatica* eggs by potential hosts simply by contributing to broader dispersal of infective eggs in the soil through its feces, or may be an even more effective agent in maintaining the host-parasite cycle through actually inhabitating and contaminating the nests of rodents. It is also possible that mice might acquire infections directly by feeding on the insect, particularly in times of food shortage. The suggestion of seasonal variation in incidence of infections shown by the present data is of interest in this connection. In all host species, peak levels tend to occur in the spring or summer months and low rates during the winter months. Higher incidence thus correlates with both a period of food scarcity in which rodents might take more insects and warm weather favoring insect activity.

With the exception of a study by Momma (1930), the possible role of insects or other invertebrates in dissemination of ova of *C. hepatica* appears to have been ignored. Momma experimentally demonstrated that flies exposed to *C. hepatica* eggs both ingested and picked them up on the body and that the ova embryonated normally after passage through the intestine of the insect. He concluded that high summer and low winter infection rates in *Rattus norvegicus* in urban areas of Japan, together with low incidence of eggs (in only 5 of 503 specimens examined) in intestines of cats used for rat extermination, was evidence that flies were the primary method of egg dissemination.

Summary

A total of 2,254 specimens of 27 species of Florida mammals was examined for infections of the liver-inhabiting nematode *Capillaria hepatica* (Bancroft, 1893). Collections were made in 22 counties of the state and in nine major habitat types.

Infections were recorded in three rodents, *Peromyscus floridanus, P. gossypinus,* and *Sigmodon hispidus,* from three widely separated localities. *P. gossypinus* constitutes a new host record for the parasite and *Sigmodon* a new record for Florida and the southeastern U.S. generally.

Over-all incidence of infection was 15.4% in *P. floridanus,* 6.3% in *P. gossypinus,* and 10.5% in *Sigmodon.* Prevalence in *P. floridanus, P. gossypinus,* and *Sigmodon* from stations positive for infections in any species was 34.2%, 14.8%, and 21.1%, respectively. Severity of infections was greater in *P. floridanus* and *Sigmodon* than in *P. gossypinus.*

Infections were largely restricted to scrub and related habitats, the rare occurrences in other major habitat types in most cases being explainable on the basis of dispersal of infected animals from scrubs. The basis of the narrow habitat specificity of the parasite in Florida, which is not apparent in other parts of its range, is unknown. Such factors as host distribution, substrate conditions, host and predator population levels, and feeding habits of hosts do not, either singly or in combination, appear to adequately account for the marked restriction of the parasite to scrub environments; and the possibility of some insect being the key factor is suggested.

In all three host species, infection rates were greater in older age classes, and in all age groups males tended to have a higher infection rate than females, although these differences were not statistically significant. Although seasonal variation in infection rates was not pronounced, incidence tended to be low in all species during the winter months, with peak levels occurring in spring in *Sigmodon* and summer in the *Peromyscus* species. Population levels and incidence of parasitism in two scrub populations exhibited an inverse relationship.

A summary of North American host and locality records of *C. hepatica* is provided.

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EXPLANATION OF THE PLATE

Plate I

Fig. 1. Normal liver of *P. floridanus* (left) and one showing lesions of *Capillaria hepatica* (right). Note lobulation of infected liver.

Fig. 2. Ovum of *Capillaria hepatica* from liver of *P. floridanus*. X625.

Fig. 3. Ova of *C. hepatica* in liver of *P. floridanus*. X300.